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ORIGINAL PAPER

Mathematical expression for the relationship between internode number and internode length for bamboo, *Phyllostachys pubescens*

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Abstract We analyzed the relationship between internode number and internode length for one of the largest bamboo, *Phyllostachys pubescens* Mazel ex Houz. For 50 sample culms with various sizes felled in a pure stand of *P. pubescens*, the internode number was assigned from base to tip and the length for each internode was directly measured. The result indicated that the internode length should be cumulated from base to tip, and then the cumulated internode length should be relativized by the total culm length. It was inappropriate to relativize the internode length by the maximum intenode length. In addition, the relationship between the relative internode number (the internode number relativized by the total number of internodes) and the relative cumulated internode length should be described not by a power function but by a sigmoid function such as the third-order function. The determined function enabled us to estimate the actual internode length, with the root mean squared error being 4 cm. In conclusion, the mathematical expression presented here, i.e., the relativization of the cumulated internode length by the total culm length and the application of the sigmoid function, will be useful in describing the relationship between internode number and internode length for *P. pubescens*.

Keywords culm form; power function; relative cumulated internode length; relative internode number; sigmoid function

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Introduction

Bamboo encompasses 1,250 species of 75 genera (Scurlock et al. 2000) and is widely distributed throughout tropics, subtropics and temperate zone of the world (Gratani et al. 2008). The bamboo culms have several interesting morphological characteristics, including the hollow part within their culms, arrangement of the vascular bundles and many nodes on their culms. Although the node is one of the most important attributes of a bamboo culm, so far the study on the nodes has been superficial and quite scarce, and thus little is known about the features of the nodes.

As shown in Fig. 1, the length of a culm segment between two nodes, i.e., internode length, was the longest at a part somewhere below the middle part of culm, and then it gradually diminished from there toward both ends of culm (e.g., Shigematsu 1940a, b; Ota 1950; Higuchi 1981). The relationship between internode number assigned from base to tip and internode length varies from culm to culm, because of the variation in culm sizes (Shigematsu 1940a; Higuchi 1981). To eliminate the effect of the size variation, the internode number and internode length are relativized by the total number of internodes and the maximum internode length, respectively (Ota 1950; Shigematsu 1940a, b). Shigematsu (1940a, b) reported that the relationship between the relative internode number (RIN) and the relative internode length (RIL) could be formulated by the combination of two or three quadratic functions. Ota (1950) also found that the relationship between RIN and RIL could be described by the Pearson's frequency function or the combination of two quadratic functions. On the other hand, Higuchi (1981) relativized the internode length cumulated from base to a given internode by the total culm length, and showed that the relationship between RIN and the relative cumulated internode length (RCIL) could be expressed by a power function, independent of culm sizes. However, these mathematical expressions have not been compared, and hence it is unclear how the relationship between internode number and internode length is described

mathematically.

The purpose of this study was thus to analyze the relationship between internode number and internode length for one of the largest bamboo, *Phyllostachys pubescens* Mazel ex Houz. First, the relationships of RIN to RCIL (Higuchi 1981) and RIL (Shigematsu 1940a, b; Ota 1950) were examined. Second, the relationship between RIN and RCIL was fitted by several functions, and their goodness of fit were compared. Third, the internode length estimated with the determined function was compared with the actual internode length.

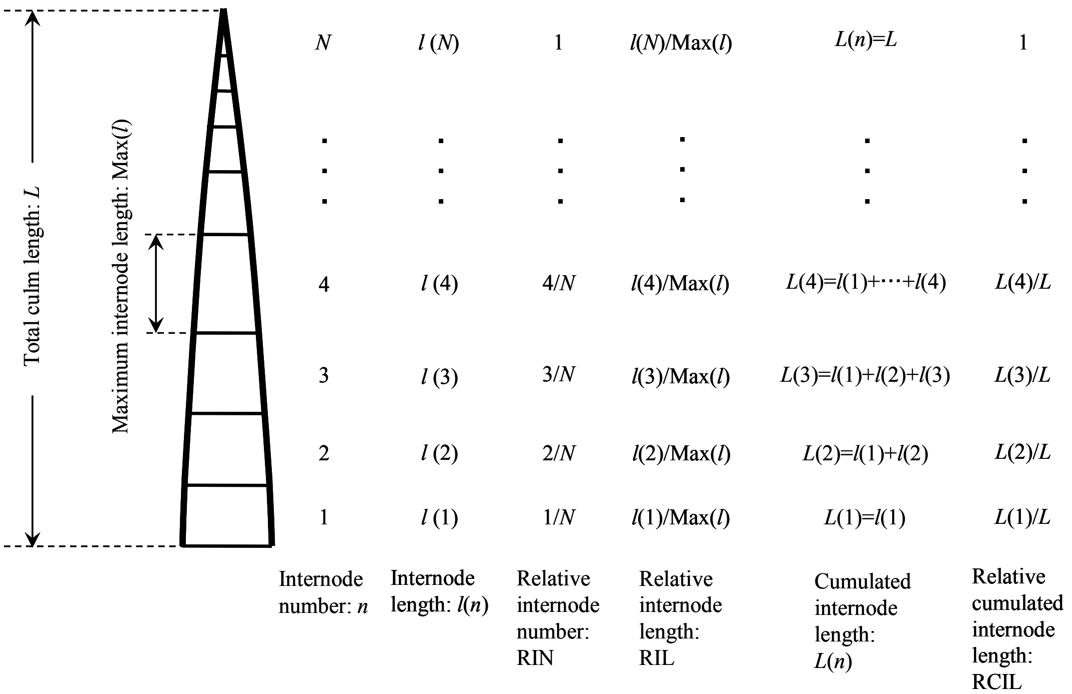

Fig. 1 Schematic diagram of the change in internode length along a culm.

Materials and methods

Data

The data used here was collected from a pure stand of *P. pubescens* in a typical Satoyama forest located in Nagomi Town, Kumamoto Prefecture, western Japan (33°04’ N, 130°62’ E). The average annual temperature and annual rainfall at the nearest observatory were, respectively, 16.0℃ and 1,866 mm, suggesting that this area will be a favorable condition for the growth of *P. pubescens* (Scurlock et al. 2000). The stand was located on a north-facing gentle slope at 35-40 m a.s.l., and was surrounded by the even-aged pure stand of *Cryptomeria japonica* D. Don and the farm land. Although this stand had been abandoned for a long time, the intensive thinning regime was performed in autumn of 2009.

In this stand, 50 healthy, living sample culms with various sizes were felled at ground level after the growing season (September 2010). The internode was numbered from culm base to tip, and then the length for each internode and the total culm length were directly measured with a tape measure. The external culm diameter at 1.2 m height above ground level (dbh) was also measured with a diameter tape. A general description of sample culms is given in Table 1.

Table 1. General description of sample culms (n = 50)

	Total culm length (m)	Diameter at breast height (cm)	Total number of internodes
Average	12.2	6.6	51
Standard derivation	4.8	2.6	10
Maximum	19.7	10.5	71
Minimum	4.7	2.0	29
Median	10.8	7.0	52

Analysis methods

To eliminate the effect of the culm sizes, the internode number and the internode length cumulated from base to a given internode were firstly relativized by the total number of internodes and the total culm length, respectively (Higuchi 1981). The internode length was also relativized by the maximum internode length (Shigematsu 1940a, b; Ota 1950). Then, the relationships of the relative internode number (RIN) to the relative cumulated internode length (RCIL) and the relative internode length (RIL) were compared. Second, the relationship between RIN and RCIL was fitted by the following functions:

Power function: $y = ax^b$ (1)

Mitscherlich function: $y = a\,(1 - \exp(bx))$ (2)

Logistic function: $y = \dfrac{a}{1 + b\,\exp(cx)}$ (3)

Richards function: $y = a\,(1 - \exp(bx))^c$ (4)

Gompertz function: $y = a\,b^{\exp(cx)}$ (5)

Third-order function: $y = ax^3 + bx^2 + cx + d$ (6)

where y: relative cumulated internode length (RCIL); x: relative internode number (RIN); a, b, c and d: parameters. An appropriately fitted function was selected by the following criteria: 1) each parameter estimate should be significant; and 2) AIC (Akaike 1974) should be the smallest among these functions. Although Shigematsu (1940a, b) combined two or three functions to express the RIN-RIL relationship, the relationship between internode number and internode length changes from culm base to tip continuously (Ota 1950). Therefore, the relationship between RIN and RCIL was fitted by a single function. Third, the length for the n-th internode, $l(n)$, was estimated from the measured total culm length, L, the total number of internodes, N, and the appropriately fitted function, $f(x)$, as follows:

$$l(n) = L\{f(\frac{n}{N}) - f(\frac{n-1}{N})\} \quad (7)$$

where $n = \{1, 2,\ldots, N\}$ and $f(0) = 0$. The estimated internode length was compared with the actual one using Wilcoxn signed-ranks test. The error of the estimated internode length was evaluated with root mean squared error (RMSE). Finally, RIN where the maximum internode length was occurred was computed for each culms. All statistical procedures were performed with the R software (R Development Core Team 2006).

Results and discussion

Figs. 2 and 3, respectively, show the relationships of the relative internode number (RIN) to the relative cumulated internode length (RCIL: Higuchi 1981) and the relative internode length (RIL: Shigematsu 1940a, b; Ota 1950) for 50 *P. pubescens* sample culms. It was apparent from Fig. 1 that the relationship between RIN and RCIL was sigmoid, and its variation was comparatively small. On the other hand, although the relationship between RIN and RIL might be concave upward, the dots were widely scattered (see Fig. 3). It will be therefore difficult to obtain an appropriate mathematical expression for the relationship between RIN and RIL compared with the relationship between RIN and RCIL. This result indicates that the internode length should not be relativized by the maximum internode length (Shigematsu 1940a, b; Ota 1950). The relativization of the cumulated internode length by the total culm length proposed by Higuchi (1981) will be effective in eliminating the effect of culm sizes.

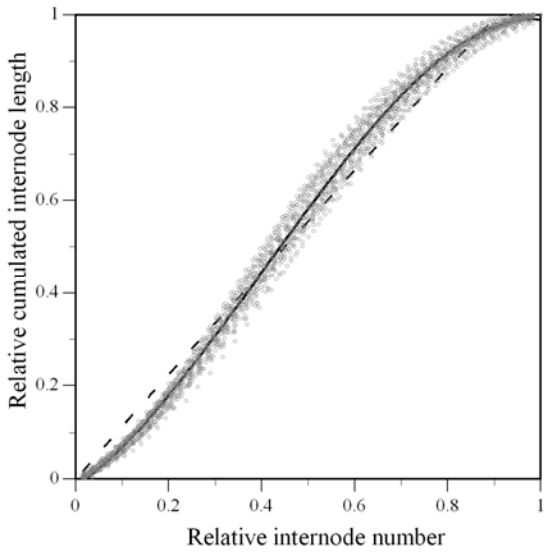

Fig. 2 Relationship between relative internode number and relative cumulated internode length for *Phyllostachys pubescens*. The cumulated internode length is relativized by the total culm length (Higuchi 1981). The solid and broken lines are fitted by the third-order and power functions, respectively.

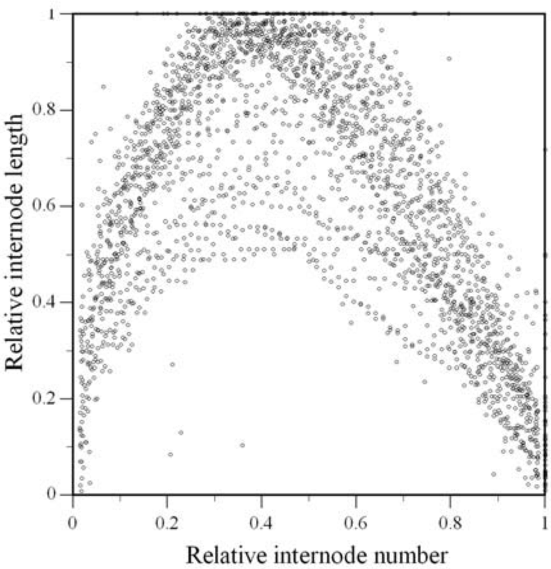

Fig. 3 Relationship between relative internode number and relative internode length for *Phyllostachys pubescens*. The internode length is relativized by the maximum internode length for each culm (Shigematsu 1940a, b; Ota 1950).

Model parameter estimates and fit statistics for the relationship between RIN and RCIL are summarized in Table 2. Because of the small variation in the RIN-RCIL relationship, all parameters for each function were significant ($p < 0.001$ for all functions). The third-order function showed the smallest AIC value compared with other functions, indicating that the third-order function is the most appropriate to express the RIN-RCIL

relationship for *P. pubescens*. By contrast, as shown in Fig. 2, the power function applied by Higuchi (1981) could not describe the RIN-RCIL relationship well. AIC value for the power function was also larger than that for the other all compared functions (see Table 2). Since the power function is a monotonically increasing function, the sigmoid relationship between RIN and RCIL could not be expressed appropriately. For these reasons, the relationship between RIN and RCIL should be expressed not by the power function (Higuchi 1981) but by the sigmoid function such as the third-order function.

The second derivatives of the third-order function, Eq. 6, is given by

$$\frac{d^2y}{dx^2} = 6ax + 2b \tag{8}$$

Table 2. Model parameter estimates and fit statistics

Model	Parameter				AIC
	a	*b*	*c*	*d*	
Power	1.103 ***	0.989 ***			-8361
Mistcherlich	6.449 ***	-0.184 ***			-8525
Logistic	1.017 ***	17.061 ***	-6.276 ***		-10763
Richards	1.254 ***	-2.391 ***	2.082 ***		-11775
Gompertz	1.122 ***	0.019 ***	-3.634 ***		-12075
Third-order	-1.390 ***	1.708 ***	0.688 ***	-0.016 ***	-12220

***: Significant at 0.1% level

Substituting the determined parameters of the third-order function (see Table 2) into Eq. 8, the internode length relativized by the total culm length increases with the relative internode number (RIN) in the half-open interval [0, 0.410). Conversely, the relativized internode length decreases with RIN in the open interval (0.410, 1). That is to say, the maximum internode length is occurred when RIN is 0.410. As mentioned above, the internode length is generally the longest at a part somewhere below the middle part of culm (e.g., Shigematsu 1940 a, b; Ota 1950). In fact, our data demonstrated that the maximum internode length for each sample culm was observed when RIN was 0.407±0.093 (mean±SD). Previous studies have also shown that the maximum internode length for *P. pubescens* was occurred when RIN was 0.466 (Shigematsu 1940a) or 0.461 (Ota 1950). These findings are approximately in accord with the estimated RIN that gives maximum internode length, i.e., 0.410, suggesting the validity of the third-order function determined in this study.

Fig. 4 compares the internode length estimated by Eq. 7 with the actual one. There was no significant difference between estimated and actual internode length (P = 0.938), with RMSE being 4 cm. This result indicates that the third-order function determined here allows us to estimate the length for each internode averagely. However, it should be noted that the internode length was often estimated to be negative when the intenode length was comparatively small. In future, it will be necessary to resolve the problem on the negative estimates.

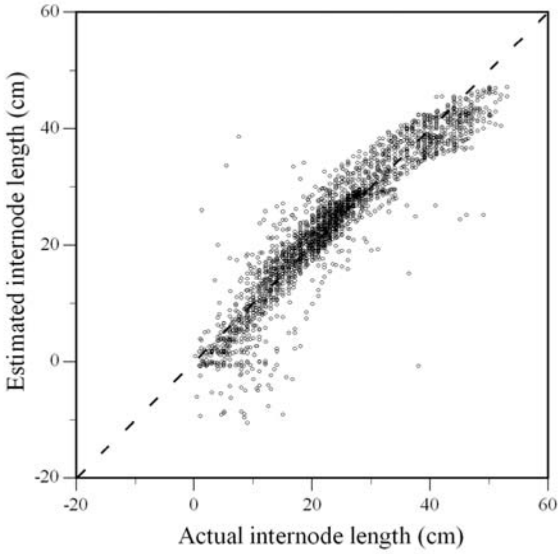

Fig. 4 Comparison of the estimated internode length with actual one. The internode length is estimated by the third-order function. The broken line indicates 1:1.

Shigematsu (1940a, 1940b) reported that the parameters of the relationship between RIN and RIL vary with culm size and species. On the other hand, Higuchi (1981) found that the variations in the parameters in the power function between RIN and RCIL (Eq. 1) are comparatively small between/within species, suggesting that RIN-RCIL relationship could be expressed by a single function, independent of culm size and species. The relativization proposed by Higuchi (1981) would enable us to eliminate both inter- and intra-specific variations in the sigmoid function as well as the power one. However, there have been no studies on the effects of site condition and culm density on the RIN-RCIL relationship. Since the results were obtained from a stand of *P. pubescens*, it is necessary to examine whether the parameters in the sigmoid function vary with stands.

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